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The role of plant physiology in hydrology: looking backwards and forwards

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Abstract

The implementation of plant physiological studies at the Institute of Hydrology focussed both on examining and understanding the physiological controls of transpiration as well as evaluating the value of using physiological methods to measure transpiration. Transpiration measurement by physiological methods would be particularly valuable where this could not be achieved by micrometeorological and soil physics methods. The principal physiological measurements used were determinations of leaf stomatal conductance and leaf water relations to monitor plant water stress. In this paper the value of these approaches is illustrated by describing a few case studies in which plant physiological insight, provided both as new measurements and existing knowledge, would aid in the interpretation of the hydrological behaviour of important vegetation. Woody vegetation figured largely in these studies, conducted in the UK and overseas. Each of these case studies is formulated as a quest to answer a particular question. A collaborative comparison of conifer forest transpiration in Thetford forest using micrometeorological and soil physics techniques exhibited a substantially larger (~ 1 mm day^{-1}) estimate from the micrometeorological approach. So the question – *Why is there a disagreement in the estimates of forest transpiration made using micrometeorological and soil physics approaches?* A range of physiological studies followed that suggested that there was no one simple answer but that the larger estimate from the micrometeorology technique might include contributions of water taken up by deep roots, from shallow-rooted vegetation and possibly also from water previously stored in trees. These sources of water were probably not included in the soil physics estimate of transpiration. The annual transpiration from woodlands in NW Europe shows a low magnitude and notable similarity between different sites raising the question – *Why is transpiration from European forests low and conservative?* An important contribution both to the similar and low transpiration is the likely reduction of stomatal conductance of the foliage associated with increasing air humidity deficit. A greater response is usually found when initial conductances are highest. Also contributing to similarities in transpiration from forest stands would be a compensatory role of understories and that deficits in soil moisture may not come into play until severe soil water deficits occur. Physiological studies have been conducted in many locations overseas. The modest transpiration of tropical rainforest is intriguing – *Why is tropical rainforest transpiration so low?* In common with temperate trees the reduction of stomatal conductance of tropical trees in association with increasing air humidity deficit will limit transpiration. In addition the high leaf area index of tropical rainforest creates conditions in the lower canopy layers that mean transpiration from those layers is much reduced from what might be possible. As well as being used to quantify and understand transpiration, physiological techniques might be used to assess when plants require water. *What is the first signal that plants need water?* Studies on sugar cane in Mauritius indicated that leaf growth was the most sensitive measure. A look forward to the future suggests that there will be a continued need for physiological measurements particularly where other techniques more suited to extensive vegetation are not appropriate. There are many unresolved issues about water use from fragmented, heterogeneous vegetation and physiological approaches are best suited to these. The measurement of sap flow in individual stems will be an important methodology in the future but there are still methodological issues to resolve.

Keywords: plant physiology, transpiration, measurement, stomata

Introduction

Evaporation from vegetation comprises the evaporation of rainfall intercepted by the canopy, interception loss and transpiration, water taken up by plant roots, passed through the plants and lost as water vapour through the stomatal pores in the leaf surfaces into the atmosphere. The interception and transpiration processes differ fundamentally in that they normally occur under very different environmental conditions. While the physical structure of the vegetative canopy and the nature of the foliage (size

and disposition) may influence interception losses, plant physiology plays no part in the control of rainfall interception loss. On the other hand, the mechanisms regulating stomatal opening, along with the environment and plant structure, are fundamental in controlling transpiration. Because interception and transpiration occur under widely different conditions, requiring very different measurement and modelling approaches, interception and transpiration are normally treated separately. Because some structural features of vegetation contribute to the control of rainfall interception, plant scientists might advise an interception specialist; however, the main challenge for plant physiologists in hydrology is related almost exclusively to the transpiration process.

Until the mid-1960s, considerable insight into the controls of stomatal behaviour under laboratory conditions had been derived from the careful work of several plant physiologists (Willmer and Fricker, 1996; Mansfield, 2004). However, little effort had been directed at making plant physiological measurements (especially stomatal conductance) in field conditions to understand and quantify transpiration from vegetation canopies. A valuable early study was that of Rutter (1967) in a Scots pine canopy. Until then, Penman's (1948) work had encouraged hydrologists to estimate evaporation from well-watered short vegetation with a universal equation. The understanding offered by Monteith (1965) emphasised that in vegetation (other than well-watered short grass) significant physiological control of transpiration can occur by regulation of the size of the apertures (stomata) in leaf surfaces. This, not incorporated in the Penman Equation, implied that, even with an unlimited soil water supply, transpiration may not proceed at rates determined by the available energy.

There can be two levels of involvement of plant physiology in hydrology and this paper will explore aspects of both. Firstly, plant physiological approaches can be used alone, where other approaches are not applicable, to estimate transpiration from vegetation. Secondly, plant physiology can be a valuable interface between other disciplines, or as an adjunct to another discipline, to give insight into the controls of transpiration. In this paper, examples of how a plant physiological input can provide stand-alone descriptions of transpiration are given in the form of narrative responses to specific questions; examples are also given to show how it can augment information from other disciplines.

Plant physiological studies at the Institute of Hydrology (IH) were initiated in July 1974 to provide an interface between the soil physics and the micrometeorological groups. This followed a collaborative study in Thetford forest in June 1973 where a discrepancy in evaporation estimates for Thetford Forest had emerged from the use of a micrometeorological technique and a soil physical one. For a whole, fairly rainless, month in June 1973, micrometeorologists had measured evaporation at the same time as a soil physics team estimated evaporation using the zero-flux plane technique. On average the micrometeorological measurement exceeded that from soil water studies by around 1 mm day^{-1}. The issue is therefore presented in the form of a question.

WHY IS THERE A DISAGREEMENT IN THE ESTIMATES OF FOREST EVAPORATION MADE USING MICROMETEOROLOGICAL AND SOIL PHYSICS APPROACHES?

The initial plant physiology studies at Wallingford were directed at explaining the Thetford anomaly. These activities were spread over a few years and investigated a number of factors that could have contributed to the discrepancy. At that time (mid-1970s), there were reports from old-growth forests in the United States (Waring and Running, 1978) that water stored in the sapwood of the trees could contribute significantly to that lost daily from the forest, most of which was derived directly from the soil; they estimated that some 27 mm in total can come out of storage in the early summer period. Clearly, evaporation of such stored water would be measured by micrometeorological techniques but not by short-term soil water physics approaches. The water coming from storage in the trees would augment water taken up from the soil and could be recharged during wet periods or in the ensuing winter. At that time, experiments at Thetford where trees were cut under water were aimed at quantifying the scale of the root resistance in mature Scots pine trees (Roberts, 1977); he argued that when the tree-cutting experiment was complete, the water bucket (in which the excised tree trunk was placed) could be removed and the contribution of the stored water to the total transpiration could be measured from the period for which the cut tree was able to sustain transpiration. Unfortunately, there was little experimental support for the hypothesis that water stored in the trees contributed significantly to the 1 mm day^{-1} discrepancy (Roberts, 1976a); the likely contribution from storage in the trees seemed to be an order of magnitude too small to account solely for the discrepancy, perhaps because the tree-cutting study took place in late summer when the trees' water content is at its lowest. Waring *et al*. (1979) found significant seasonal changes in water content of Scots pine stands of varying tree spacing/stand density; for a woodland of tree density similar to that of Thetford, the maximum stored water was around 12.5 mm. While there is a possibility that, in the initial part of the early summer

(June 1973) study at Thetford, up to 1 mm day^{-1} might have been available from storage in the trees, this could not sustain or augment transpiration for more than a few days. Certainly, it could not be the sole source of water at the rate of 1mm day^{-1} over an entire month.

While a soil physics approach might well underestimate losses from surface soil layers, the measurements in June 1973 minimised any likelihood of under-estimation of surface losses. However, the contribution of the litter layer and the undergrowth at Thetford had to be determined. By June of each year a bracken understorey develops at Thetford and in midsummer transpires vigorously; further, even before the bracken emerges and after it has senesced, evaporation losses from the litter layer might be significant. Detailed observations of the transpiration from the bracken understorey in the forest were made from May to October 1976 (Roberts *et al*., 1980). The leaf area of bracken is not fully developed in June and the fractional contribution of bracken to total forest transpiration, 22% in June, rose by August to 57%. Overall, these percentages amount to much less than 1 mm day^{-1} and so the understorey contribution cannot be the single answer to the discrepancy in transpiration; however, the studies demonstrated a major role for understoreys in forests at certain times and showed how plant physiological approaches offer a means of estimating water use which is not possible by traditional hydrological approaches. Moreover, in whole forest transpiration, an understorey might compensate for a reduced contribution from the tree component, either because of reduced tree densities or smaller leaf area of a less vigorous species. In a further study in Thetford Forest, Roberts *et al*. (1982) showed that the bracken understorey in a Scots pine stand compensated for the lower tree transpiration of the Scots pine trees, as compared with transpiration by Corsican pine in a vigorous Corsican pine stand with no understorey.

In estimating soil water abstraction by deep-rooted vegetation by soil physical methods, it is essential that soil moisture measurements are made over the whole rooting depth of the vegetation. An additional problem at Thetford was the significant spatial heterogeneity of the soils which might have allowed some deep roots to access the chalk directly via sand-filled discontinuities in the otherwise unrooted chalky glacial drift. Figure 1 shows a section of a typical soil profile at Thetford (Roberts, 1976b) and illustrates a sandy incursion reaching the geological chalk. It is conceivable that individual trees could access water from the chalk via deep roots. Water taken up in this way might not be measured by the soil physics approach but would be included in a micrometeorological determination.

While not in any sense suggesting that, in all circumstances, estimates of transpiration made from changes in soil moisture content will be erroneous, some areas have been identified where caution is required if a soil water balance approach is to be employed with confidence. The problem with the soil moisture approach might be greatest in estimating rapid changes in soil water content. The loss of water from litter layers (e.g. Rutter, 1966) and understoreys (Roberts *et al*., 1980) cannot be neglected and soil water studies must sample changes adequately in the uppermost soil layers. For plantation woodlands in the UK, the contribution to short-term transpiration losses from water stored in trees is rather small but in 'old growth' forests — whether in temperate or tropical regions — transpiration from such stored water should not be disregarded in short-term studies. The use of changes in soil moisture to quantify the water use of vegetation must acknowledge the soil depths from which plants can acquire water. There might always be a problem in spatially heterogeneous soils, as illustrated for Thetford above, but there is also an issue in soils underlain by chalk. In such soils, substantial upward movement of water can occur from the chalk matrix to overlying soils, without the presence of roots. (Wellings and Bell, 1980; Roberts and Rosier, 2005a). Therefore, instrumentation to monitor soil moisture changes must be installed to a depth significantly greater than that penetrated by roots.

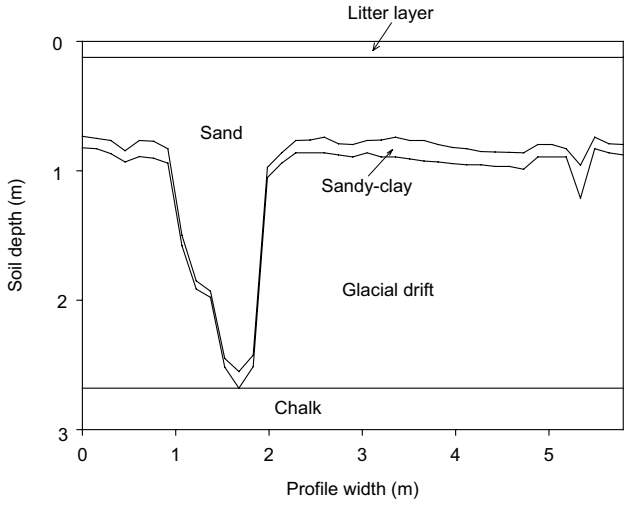

Fig. 1. *An example of the soil profile beneath the forest at Thetford, UK (after Roberts, 1976b) illustrating a sandy incursion reaching the geological chalk.*

WHY IS TRANSPIRATION FROM EUROPEAN FORESTS LOW AND CONSERVATIVE?

In the 1970s and 80s, IH (e.g. Gash *et al*., 1980) measured evaporation losses from rainfall interception by UK forests.

This required a literature survey (Roberts, 1983a) of transpiration losses from woody species that constitute UK woodlands. Because the data from UK forests was so sparse, reports from European forests were included where they referred to species that grew in UK forests; the small and rather similar estimates of forest transpiration in Europe were noted and possible explanations were proposed for the similarity of annual transpiration over a range of sites, climates, years and species (both broadleaved and evergreen).

Without establishing the exact mechanism, numerous reports have shown a strong negative relationship between leaf stomatal conductance (g_s) and air humidity deficit (D). There is also evidence that species with initially high conductances respond more sensitively to increases in air humidity deficit. These responses will modulate the levels of transpiration and may reduce differences between species. Figure 2 presents data from Federer (1977) which show the g_s versus D response for several tree species from the north-eastern USA. All species show a decline in g_s with D, with the biggest response in the species with the highest initial g_s. A similar response has been observed widely in forest trees under field conditions in the UK. Figure 3 shows the decline in g_s versus D in three canopy layers in ash and beech woodland at Black Wood, Hampshire; it tends to modulate transpiration in the environmental conditions most likely to produce high transpiration and demonstrates the greater sensitivity of the upper canopy layers that have the highest conductances.

Also contributing to similarity in woodland transpiration would be the presence of an understorey. It has already been seen that an understorey can make an important contribution

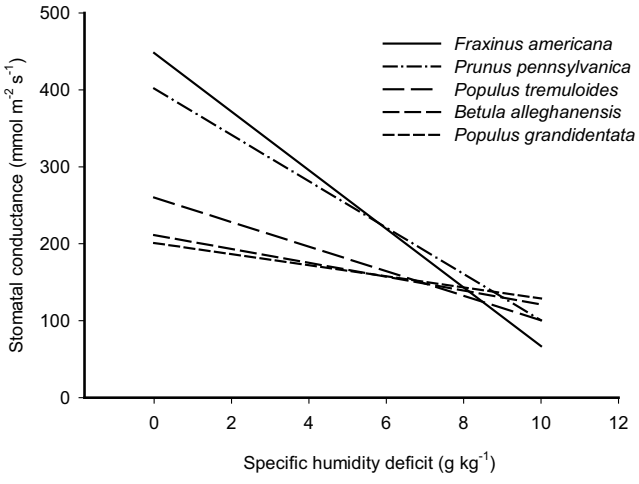

Fig. 2. *Variation in stomatal conductance gs with air humidity deficit D in five woody species (after Federer, 1977). Include mention of gs and D, as in text above.*

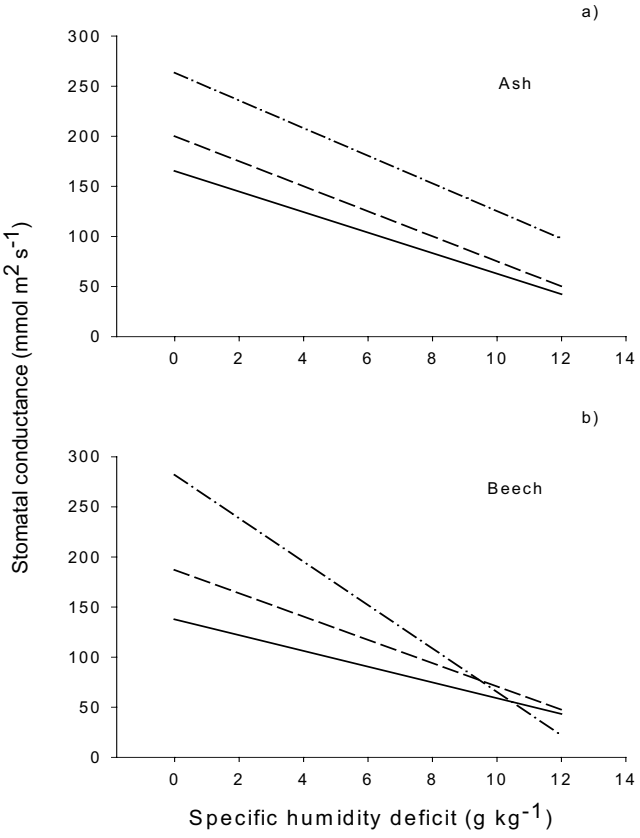

Fig. 3. *The decline in stomatal conductance gs with air humidity deficit D in a) ash and b) beech growing at Black Wood, Hants., UK. For both species data is shown from the upper canopy (— × —); middle canopy (– – –) and lower canopy (——) (after Roberts and Rosier, 1994). Include mention of gs and D, as in text above*

to total forest transpiration and can minimise differences between a vigorous woodland of trees alone and a less vigorous woodland that also supports an understorey.

It is commonly supposed that forest transpiration will be restricted by lack of soil water. It might therefore be expected that, in a range of transpiration studies from north-west Europe, some variation might be generated by spatial and temporal variation in soil water conditions which would affect transpiration. Whilst soil moisture variability is known to influence transpiration of young trees, the relevance of these studies to adult forest trees must be questioned. Reports of reduced soil moisture influencing transpiration in adult forests are far less common. A review of forest transpiration by Rutter (1968) showed that in forests with an intrinsically high transpiration rate, only modest reductions in soil moisture lead to a reduction in transpiration (Fig. 4a). Conversely, he also showed (Fig. 4b) that, where transpiration is modest, a large fraction (~70%) of the available soil moisture can be removed before transpiration rate is reduced. Examples of the type of response in Fig. 4a were observed in the UK in a study of transpiration of short

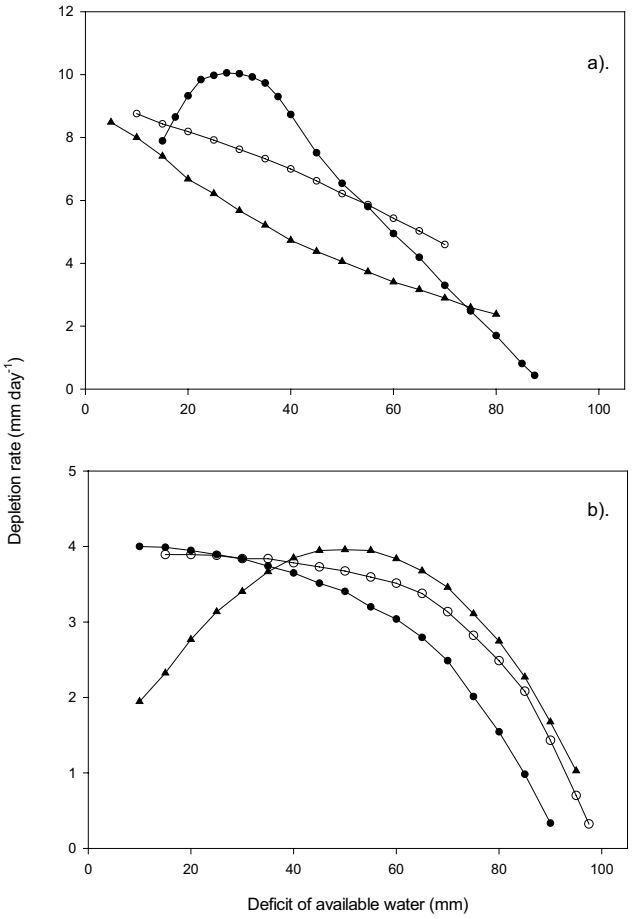

Fig. 4. *The variation in soil water depletion (transpiration) with deficit of available water in three studies with high depletion rates (a) and three studies with low depletion rates (b) (after Rutter, 1968).*

rotation coppice (Allen *et al*., 1999). When well supplied with water, transpiration was high. The response in Fig. 4b was found by Stewart (1988) for Scots pine at Thetford, where transpiration was rather conservative.

In summary, the low and very similar transpiration rates from European forests are probably explained by a combination of circumstances. In most woody species used in forestry (species such as poplar and willow used for short-rotation coppice are exceptions), a strong negative feedback between g_s and D will reduce transpiration. Soil moisture levels are likely to be of lesser importance. Because of the role of understorey transpiration, structural differences between forests are probably less important in producing transpiration differences.

WHY IS TROPICAL RAINFOREST TRANSPIRATION SO LOW?

Anticipating the worldwide interest in evaporation from tropical rainforest and the links to global climate, IH established studies of evaporation and energy partitioning in tropical rainforest in the central Amazon close to Manaus in Brazil (Shuttleworth *et al*., 1984a, b, c). In terms of plant physiology, the important scientific objectives were to determine (i) the important environmental controls on rainforest transpiration and (ii) rainforest transpiration and the major sources of transpiration in the canopy.

Physiological studies embedded within the main IH project at Manaus measured vertical variation in leaf stomatal conductances on foliage accessible from a tower in the forest. Because potential evaporation was high, daily transpiration from tropical forest was also likely to be high. On an annual basis, transpiration was indeed high (>1000 mm in 1984; Shuttleworth, 1988) because the canopy is evergreen and evaporation continues throughout the year. However, average daily transpiration was modest (~ 3.6 mm day^{-1}; Shuttleworth, 1988); it differs little from rates observed in midsummer in temperate broadleaved or coniferous woodland in Europe. Why is this so?

Some of the first observations of stomatal conductance (g_s) through the canopy of a tropical rainforest (Roberts *et al*., 1990) illustrated important physiological features of canopy physiology that have a fundamental bearing on the explanation of the rather low rates of daily transpiration observed in this Amazonian rainforest. A subsequent synthesis (Roberts *et al*., 2005a) of numerous studies of rainforest transpiration indicated that the results from Brazil were by no means exceptional; similar behaviour has been reported from tropical rainforests in other continents. The first important feature was that g_s decreased with canopy depth; light intensity was more important than any species difference (Fig. 5). Because of the constraints on extensive

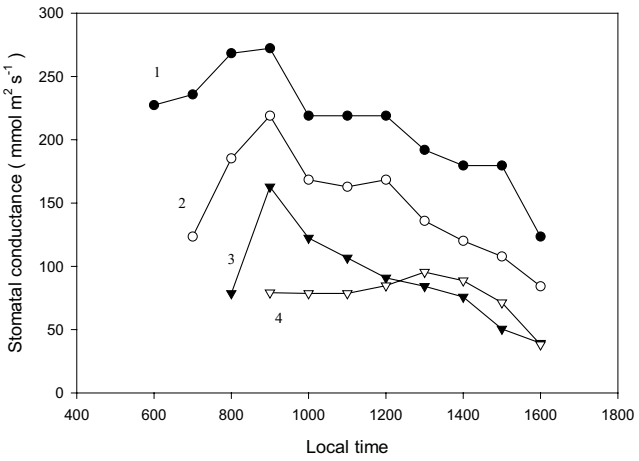

Fig. 5. *The mean diurnal variation in stomatal conductance of four species with canopies distributed vertically through a central Amazonian rainforest, Brazil. 1).* Piptadenia suaveolens *at 33m; 2).* Licania micrantha *at 25.6 m; 3).* Naucleopsis glabra *at 17 m; 4).* Scheelea *species at 3 m (after Roberts* et al.*, 1990).*

horizontal sampling imposed by a single tower at the site in Manaus, the result could not be proven at one location. However, other studies in tropical rainforest (McJannet *et al.*, 2006) have indicated from sap flow measurements that it is tree size (and hence the vertical disposition of its canopy) rather than species differences that is the major determinant of the level of transpiration.

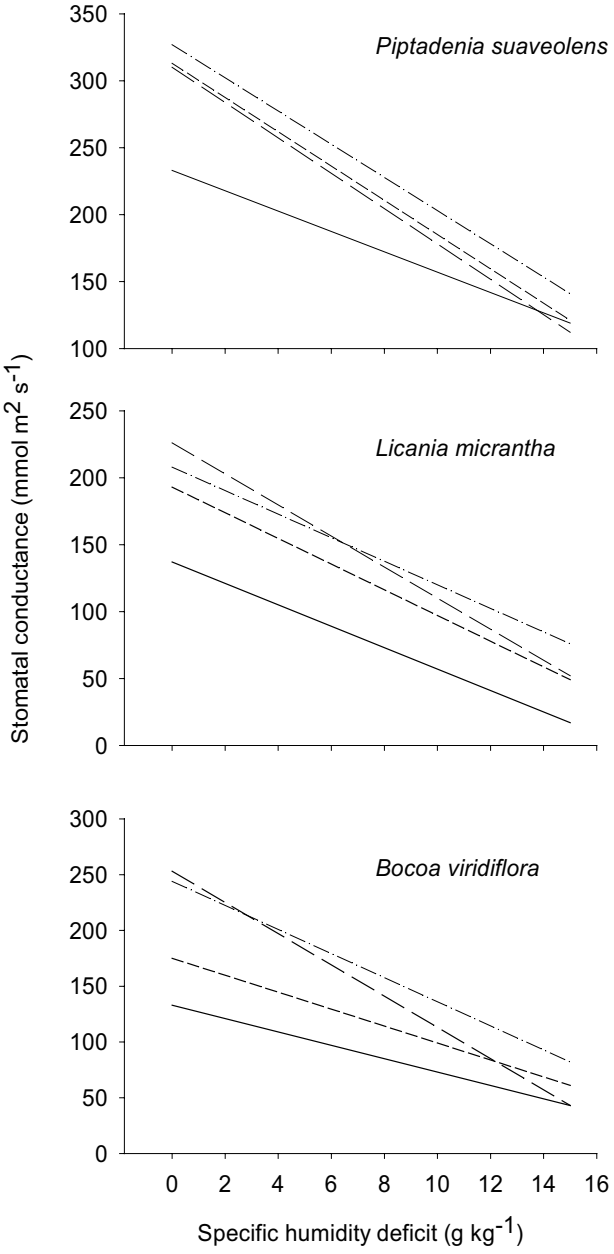

Fig. 6. *The decline in stomatal conductance with air humidity deficit in three tree species of the canopy of a central Amazonian rainforest.* Piptadenia suaveolens *at 33m above the ground;* Licania micrantha *at 25.6m and* Bocoa viridiflora *at 23m. Fitted regressions are shown for data taken in radiation class 601-700 W m^{-2} (— × —); 501-600 W m^{-2} (— —); 401-500 W m^{-2} (– – –) and below 400 W m^{-2} (——) (after Roberts* et al.*, 1990).*

Examination of the relationship between g_s and environmental variables also revealed a strong negative relationship between g_s and D in the trees that predominated in the upper canopy (Fig. 6). This occurs also in many cases of temperate woodlands and other vegetation Although solar radiation, temperature and D all increase up to noon or mid-afternoon, the steady decline thereafter in g_s (Roberts *et al*., 1990) and, therefore, unsurprisingly, in canopy conductance (g_c) (Shuttleworth, 1989), means that transpiration is maintained at modest levels.

There is a further constraint on transpiration from tropical rainforest which reflects the very nature of tropical rainforests in which continuous dense foliage is distributed from the upper canopy regions down to ground level. Leaf area indices of around 6 m^2 m^{-2} are common in tropical rainforest although values as high as 12 have been reported (Roberts *et al*., 1996). Such high density of foliage might, at first sight, have the capacity for high transpiration but the high leaf area has compensatory influences which moderate transpiration. Low light levels, low wind speeds and low vapour pressure deficits in the lower canopy regions mean that stomatal conductance in the foliage in the lower canopy layers will be low as will evaporative demand. In contrast, the foliage in the upper parts of the canopy will be exposed to high levels of radiation, and will exhibit high stomatal conductances where the foliage is exposed to high evaporative demand conditions (high *D*, significant available energy and moderate windspeeds). Therefore, despite the considerable amount of foliage in the lower parts of tropical rainforests, the transpiration from these zones is limited by the very conditions that they, and the foliage immediately above them, create. Roberts *et al.* (1993) showed (Fig. 7) that although the upper canopy layer comprises less than 2% of the leaf area index (L*), it produces over 10% of the transpiration. On the other hand, the lowest canopy layer is nearly 35% of the L* and is responsible for only 8% of the transpiration.

DO SOIL MOISTURE LEVELS INFLUENCE FOREST TRANSPIRATION?

Uncertainty still remains about the influence of long dry periods in summer on the transpiration of woodland under UK conditions. There are several important reasons why this uncertainty must be reduced. One is that more needs to be known about the impact of woodland on recharge. However, this question is relevant under all conditions, not only when droughts prevail. Furthermore, increasing certainty of the impacts of global warming and changing climate raises questions, such as what soil/tree species combinations are more or less susceptible to severe droughts.

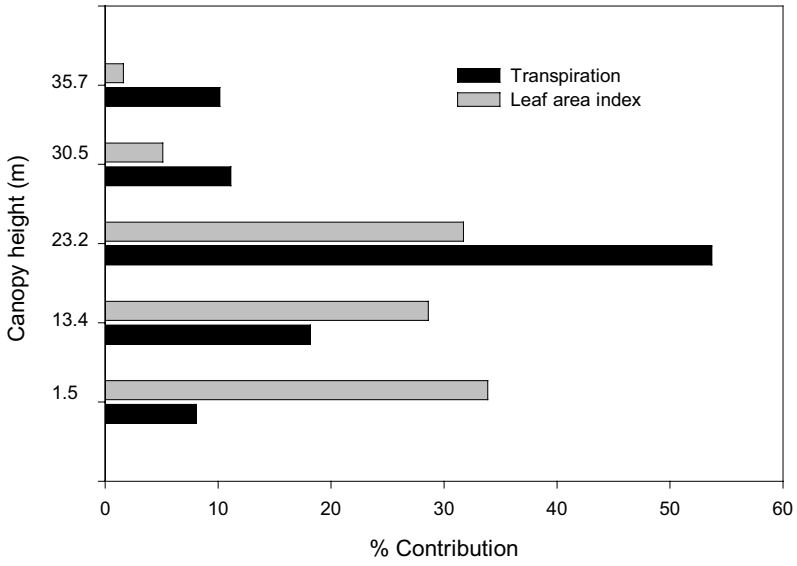

Fig. 7. *Variation in the fraction of leaf area index and of total transpiration contributed by five canopy layers in a tropical rainforest in the central Amazon, Brazil (after Roberts* et al.*, 1993).*

Some of the detailed work, including physiological measurements on ash and beech growing on clay and chalk soils gives some insight to the woodland interactions with soil water levels on these different soils. In one study, measurements of stomatal conductance were made on ash at a chalk site (Black Wood, Hampshire) in 1989 (Roberts and Rosier, 1994) and at a clay site (Old Pond Close, Buckinghamshire) in 1990. The years 1989 and 1990 had hot dry summers. Figure 8 shows the summer average stomatal conductance in upper and lower canopy levels at both sites in 1989. The upper canopy of the ash at the chalk site retained a high stomatal conductance in that summer. The behaviour of beech (Roberts and Rosier, 1994) was very similar. At the clay site, low levels of stomatal conductance prevailed at both canopy levels, indicating that the soil water deficits were critical for the trees. At the chalk site, Black Wood, even though the surface soils were dry, water may well have been moving up through the chalk to satisfy the water demands of the woodland. Indeed, this upward water movement in the chalk matrix could occur without roots being present in the chalk.

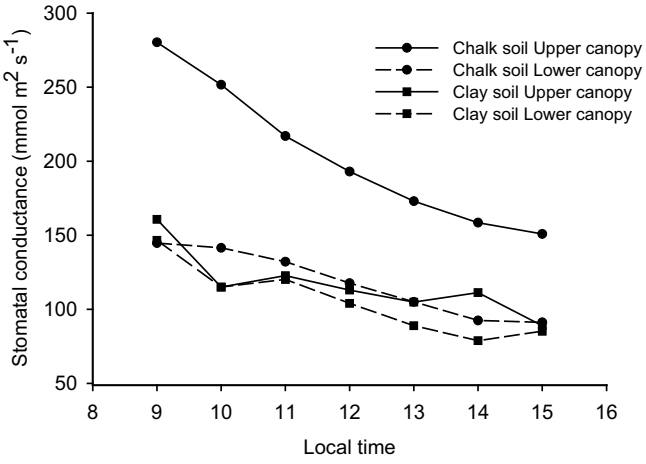

Fig. 8. *Average diurnal trends of stomatal conductance of ash woodland growing at two sites (Chalk site, Black Wood, Micheldever, Hampshire) (Clay site, Old Pond Close, Olney, Buckinghamshire) (unpublished data).*

Changes in water content of chalk soils should normally be interpreted with associated soil water potential profiles. This will enable soil moisture changes to be interpreted correctly as either upward movement or drainage. A recent study (Roberts and Rosier, 2005a) revealed that the Calder *et al*. (2000) interpretation of soil water changes below beech woodland at Black Wood included drainage losses with the upward water movement and so overestimated forest water use substantially. The most recent work at Black Wood (Roberts and Rosier, 2005a, b; Roberts *et al*., 2005b) showed that extensive areas of broadleaved woodland use no more water overall than adjacent grassland. Both sites have chalk soils and the maintenance of a soil water supply from the chalk to the grass in dry conditions is also likely to be an important factor in minimising differences between woodland and grass.

Some gloomy predictions have been made about the future of common UK trees, especially the shallow-rooted beech, if summer droughts become more frequent and severe (Harrison *et al*., 2001). These predictions have overlooked

the special properties of chalk, a geological formation beneath large areas of beech in southern UK. The upward movement of water from the chalk means that the shallow-rooted nature of beech is less of a problem than it might be on soils without underlying chalk.

A further unsuspected feature of chalk subsoils and their implications for possible drought stress to shallow-rooted vegetation was found at Black Wood after the very wet winter of 2000/2001; a large 'reservoir' of water accumulated in the upper layers of the chalk as it moved slowly down the chalk profile (~1m year^{-1}). This water was accessible for upward movement in response to water potential gradients in subsequent summers, perhaps associated with significant droughts. This long-term dynamic storage aspect of the chalk and its relationship to the hydrological functioning of planted and natural vegetation on shallow soils above chalk, deserves thorough investigation.

WHAT IS THE FIRST SIGNAL THAT PLANTS NEED WATER?

Much IH research on physical processes was focused on the consequences of land-use change on water resources, both in the UK and in East Africa. It was essential to obtain a better understanding of the physical and physiological processes by which evaporation from different vegetative types occurred and the amounts of water lost. Hence, IH collaborated with the Mauritius Sugar Industry Research Institute (MSIRI) in a joint project to maximise the efficiency of drip irrigation of sugar-cane. The feasibility of using tensiometers to measure soil water potential to monitor the need for irrigation water was explored. In a parallel study, plant physiological techniques were also used to evaluate the need for the sugar-cane to be irrigated. Although measurements of leaf water potential will show when reductions in soil water lead to water stress in plants, these measurements do not necessarily reveal whether a threshold level of plant water stress has been reached, and whether growth processes have been compromised so that irrigation is essential.

Several plant physiological measures show whether a plant is water stressed: of these, both stomatal conductance and leaf photosynthesis are easily measured with portable field equipment. Both of these, as well as plant water potential, were measured in plots of sugar-cane receiving excess, optimal and inadequate supplies of irrigation water. Following the seminal review of water deficits and plant growth by Hsiao (1973), measures of leaf growth (and, in particular, of leaf extension which might prove to be a very sensitive indicator of the influence of the reduction in soil water supply) were included in the suite of measurements used to evaluate the effect of different levels of irrigation on the physiology and growth of sugar-cane.

Sugar-cane is a particularly suitable plant on which to measure leaf extension. New leaves emerge frequently during the major period of growth which in Mauritius occurs in the usually dry period from September to December when irrigation is necessary. In a situation such as Mauritius, where labour is cheap and plentiful, daily monitoring of irrigation need by measuring leaf extension at daybreak and dusk, is a very feasible option for monitoring irrigation need. This involves measuring the length between the leaf tip and the leaf ligule or dewlap (a membrane or hairy tuft that occurs in grasses in the angle where the leaf blade joins the stem. At that time of the year young leaves are extending night and day and daily extension of 50 mm is not exceptional.

Results illustrating the relative sensitivity of different plant physiological measures to reduction in water supply are shown in Table 1. In this study three treatments were compared: (a) rainfed conditions only; (b) irrigation equivalent to the previous ten days potential evaporation (*ET*) applied as single application at the beginning of the study; and (c) an application of the previous days' potential evaporation applied early each day. Table 1 compares the 10-day and daily *ET* treatments for leaf extension in the night and in the day as well as stomatal conductance (g_s) and leaf net photosynthesis (P_n). The most sensitive measure

Table 1. A comparison of sugar cane treatments irrigated either each day with the equivalent of potential evaporation (1.0*ET*) or once at the beginning of the study with ten times the average potential evaporation (10 × *ET*). Entries in the cells of the table (>) indicate when significant differences develop between treatments for leaf extension (2 entries for day and night), stomatal conductance (g_s) and net photosynthesis (P_n).

Date in 1987	*Day/Night*	1.0 *ET*	10 × *ET*	1.0 *ET*	10 × *ET*	1.0 *ET*	10 × *ET*
		Leaf extension		g_s		P_n	
2/12	D/N	=/=		=		=	
4/12	D/N	>/=		=		=	
8/12	D/N	>/>		>		=	
11/12	D/N	>/>		>		>	

of the plants' need for soil water was the leaf extension between 06:00 hr and 18:00 hr. Stomatal conductance and especially leaf photosynthesis were less sensitive; for example, when leaf photosynthesis measures indicated that irrigation was required on 11 December, daytime leaf extension had signalled this need one week earlier, on 4 December.

However, leaf extension may not always be a suitable measure of how plant growth is limited by a reduction in soil water availability. In temperate broadleaved and coniferous trees, leaf and shoot expansion occurs over a relatively short period in spring when soil water is usually plentiful. In such cases, leaf extension may not offer a useful measure of how soil water deficit affects plant growth. However, leaf extension might well prove to be a useful indicator of the suitability of hydrological conditions for grasses and other monocotyledonous plants commonly found in wetland habitats.

The future: some problems

Notwithstanding the techniques that are available to make measurements, important uncertainties remain about the transpiration (and interception) of particular vegetations, both overseas and in the UK. In the past three decades or so, benchmark micrometeorological studies have been established in what might be regarded as elite sites, usually on flat terrain covered with extensive uniform vegetation. Studies established by IH in Thetford Chase, East Anglia (Stewart and Thom, 1973) and the Reserva Ducke, Manaus, Brazil (Shuttleworth 00:*et al*., 1984a,b,c) are good examples.

Often there are discontinuities and heterogeneities in natural, established and cultivated vegetation. Then, even the most modern micrometeorological techniques may not be appropriate and so physiological approaches, such as sap flow techniques, may be used to measure and understand the controls of transpiration by such vegetation. A feature of lowland UK is the patchwork of woodlands dispersed in the landscape. Evaporation (both of water intercepted by the vegetation and transpiration) is likely to be enhanced at woodland edges (Kinniburgh and Trafford, 1996) but the extent of the edge effect is unknown. It is likely that transpiration loss will only be determined from sap-flow measurements on representative individual plants, at sites from near the edge to well inside the woodland. The limited information available about edge influences is also reflected in the lack of knowledge and understanding about the hydrology of fragmented woodlands in the landscape. Hedgerows and wet woodlands are important examples of fragmented woodland.

There is also limited knowledge about the influence of canopy heterogeneity on water use (both transpiration and interception). While edge effects have been shown to be important in determining water use in woodlands, in forests and woodlands bigger and smaller 'edges' exist in the woodland canopy, by virtue of the proximity of species of different growth rates or of the same species of different ages. Figure 9 illustrates homogeneity and heterogeneity in two broadleaved woodlands. Real woodlands can be identified that compare with the two examples given in the figure. That represented in Figure 9a might be observed typically in woodland under traditional management in which a subset of trees from the even-aged woodland are harvested and the canopies of the existing trees are allowed to exploit the newly-available space. A management practice currently favoured in UK forestry is continuous cover forestry (CCF), in which individual trees are harvested and young trees are encouraged to grow in the suitable gaps that are created. This is likely to lead to a heterogeneous canopy structure as in Fig. 9b. At present, it is difficult to predict the hydrological impact of these different styles of management and sap flow techniques might have an important role in resolving transpiration differences at the scale of the individual trees in such contrasting woodlands. Detailed plot studies of transpiration and interception are needed, with catchment-wide assessments of key structural attributes controlling evaporation such as sapwood cross-sectional area and leaf area index.

Apart from the effects on hydrological regime associated with site preparation and canopy closure (Robinson, 1998; Robinson *et al*., 1998) there is accumulating evidence that the age of a forest stand influences evaporation. The best example of this phenomenon comes from the catchments covered in mountain ash (*Eucalyptus regnans*) forests near Melbourne, Australia. From a combination of studies including fluctuations in stream flow and detailed process studies (Langford, 1976; Cornish, 1993; Kuczera, 1985, 1987; Vertessy *et al*., 1993, 1997; Watson *et al*., 1999) it has emerged that water use is greatest in young, vigorous stands and declines as the forest reaches maturity and beyond. In UK forest conditions, trends from streamflow records at Plynlimon suggest that evaporation from maturing forests may be less than that from younger plantings (Hudson *et al*., 1998; Marc and Robinson, 2007). However, it is not possible to give good estimates of evaporation, and hence of streamflow responses, in a landscape where trees are of varying ages.

Compared with the UK, far greater attention has been paid in the past to the dynamics of water movement and loss from forest litter in the United States and Canada (Kittredge, 1940; Mader and Lull, 1968; Finney and Martin, 1993). One major reason for this interest is the vital role of litter and its

Fig. 9. *A schematic diagram showing the contrast in canopy structure between an even-aged broadleaf woodland with regular thinning (above) and an uneven aged woodland with selective thinning (below).*

dryness as a forest fire hazard. There is a number of reasons why more needs to be known about the dynamics of water movement in litter layers of UK forests, especially those in the uplands.

There is an interest in the role that forests play in the mitigation of flood risk. For UK conditions it is not easy to predict the effects of forest litter in modulating flow regimes in forests, nor how forestry practices that alter the amount of litter (e.g. by harvesting whole trees or otherwise) play in the hydrology of the soil surface zones. Furthermore, some predictions of climate change envisage greater frequency of dry summers and of wetter winters. One of the consequences of prolonged droughts may be increased drying of the litter layer, with the likelihood that subsequent storms are more readily shed from its surface until the litter becomes rewetted and permeable. Such a scenario must remain speculative until there is more information from carefully-designed field studies.

Arguably, studies of evaporation and its controlling processes in both upland and lowland areas in the UK have focused largely on forests and woodlands, rather than vegetation such as bracken or heather moorland. For grassland, the Penman estimate (Penman, 1948) is traditionally regarded as suitable for all well-watered grass. A preliminary study (Roberts 1983b) showed differences of up to 30% in transpiration between improved pasture and unimproved pasture, dominated by upland grasses such as *Nardus stricta*. Such studies deserve to be repeated and extended. Information is now emerging (Sparks *et al*., 2005) that grass (lawn grasses in this instance) is growing for longer periods in the year. The hydrological effects of a longer growing season for upland and lowland pastures is unknown and deserves attention.

At a number of places in this paper, the relevance of the link between stomatal conductance (g_s) and air humidity deficit (D) has been mentioned. This link is purely correlative but has proven robust enough for use in numerous modelling studies. The exact mechanism of the control of g_s and the role of D remains to be revealed. There is reasonable evidence (Monteith, 1995) that transpiration rate rather than D constitutes the over-riding control. Given the importance of the controls of g_s to land surface exchanges, including transpiration, better descriptions of stomatal function in mechanistic, non-empirical terms would be welcome.

The future: some methodologies

No appreciation of the value of IH's contribution to hydrological research under Dr. McCulloch's leadership would be complete without mention of his recognition that, in common with other areas of science, advances in hydrological knowledge need robust instrumentation for reliable measurements under field conditions. Moreover, emerging questions on the role of plant physiology in hydrology require instruments as yet unavailable. Much of the understanding of the transpirational behaviour of vegetation in the natural environment has come from painstaking measurements within and through vegetation canopies using porometers and portable infra-red gas analyzers (IRGAs). These equipments no doubt have still an important role to play. Because IRGAs are also able to resolve CO_2 exchange issues, their continued use for *in situ* CO_2 exchange, for example of soils as well as leaves, will be invaluable in the future.

However, many of the problems faced by plant physiologists concerned with plant water use are best addressed by measurement of transpiration at the leaf and plant scale; these lead to problems in sampling and scaling which are even greater at the plot, hillslope or catchment scales, when the physiological responses of many different vegetation types have to be aggregated.

The flow of sap for the purpose of determining transpiration losses from individual trees was first measured directly in the early part of the last century (e.g. Huber and Schmidt, 1937). Nevertheless, it is only over the past two decades that sap flow of plants, especially trees, has been measured routinely and reliably. Approaches to the measurement of sap flow have been reviewed critically by Smith and Allen, (1996) but there are still areas where development is needed in the next few years, if sap flow approaches are to be used even more routinely than at present.

Estimating transpiration by sap flow requires numerous assumptions. While the stem heat balance method (Sakuratani, 1981) might be recommended with confidence, there are limits to the size of sensors that are available and, therefore, to the size of stems (generally <35mm in diameter) that can be monitored. Other sap flow methods that use probes that are installed directly into the tree also raise important concerns. These include the effect of injury to the stem, the cross-sectional radial distribution of sap flux, and how this is related to the measurements made by the sensors. The variation of sap flux around a particular stem and how that can be sampled adequately is also unknown. A major shortfall in many studies and one that should be addressed seriously is careful *in situ* calibration of sap flow sensors. Roberts *et al*. (2001) used Granier thermal dissipation probes to measure transpiration over two seasons in a mature beech wood. Laboratory calibration of the sensors was widely divergent from the calibration proposed by Granier (1985). A fresh calibration, and scaling for tree size in the beech woodland, resulted in excellent agreement between transpiration estimates made on numerous dry days in 1999 and 2000 with measurements by sap flow and eddy correlation techniques (Fig. 10; Roberts *et al*., 2001). These results, corroborated by measurements of soil moisture content and soil potential (Roberts and Rosier, 2005a)

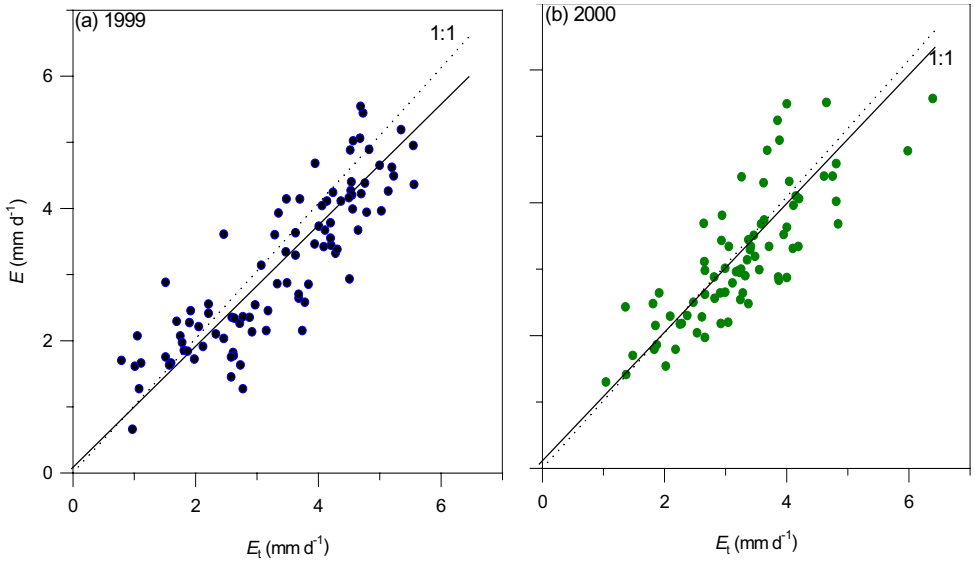

Fig. 10. *The correspondence on dry days between tree transpiration (*E_t*) determined with sap flow sensors and evaporation (*E*) measured with an eddy correlation device at a beech wood, Black Wood, Hants., UK. Data are shown from 1999 (a) and 2000 (b) (after Roberts* et al.*, 2001).*

confirmed that transpiration from the woodland was supported by upward movement in the chalk subsoil, even when the surface soils had developed a substantial negative soil water potential. There may be a need to measure transpiration of isolated trees in natural landscapes but there is also a requirement to improve knowledge of the water requirements of trees in urban environments (Roberts *et al*., 2006b). Unfortunately the deployment of sap flow equipment on several large isolated trees not necessarily growing close together would demand different equipment to a forest situation**.** There is not yet readily available a high resolution (mV) miniature data logger (~ 5 channels) plus heating system that is cheap enough to be dedicated to measurements on individual isolated trees. Such a device is eagerly awaited by researchers of water use by urban or savannah trees.

Apart from the smallest stem heat balance gauges that have been used on grass stems (Senock and Ham, 1993), physiological techniques are in short supply to measure short, non-woody vegetation, such as low grass swards. These occur in small patches that would be particularly unsuitable for micrometeorological techniques. A promising technique that needs much fuller evaluation is an evaporation chamber method of the type reported by Kohsiek (1991). This device comprises a transparent Perspex box inside which is a ventilation fan and fast response humidity sensors connected to a data logger recording every second. The chamber is placed over short vegetation for short periods and the surface conductance or transpiration can be determined from the rise to a new equilibrium level of relative humidity in the chamber. A determination takes a few tens of seconds. Such a device enables determinations to be made in situations where porometers, IRGAs or sap flow approaches are inappropriate.

The value of using plant physiological techniques both to measure transpiration and to understand its controls has been demonstrated in a number of case studies. There will be a continuing need for this in the future, particularly where transpiration information is sought about fragmented and heterogeneous vegetation, not suited for study by micrometeorological and soil physics approaches. To fulfill this need, measurement techniques that resolve fluxes at the leaf and plant scale will need to be relied upon to provide accurate results.

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